
THE DEVELOPMENT OF THE SPORANGIUM OF EQUISETUM HYEMALE.*

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The sporangium of *Equisetum* has been the subject of considerable study. The first work of importance was by Hofmeister who seems to refer the whole of the sporangium to a single cell. Later Russow while verifying many of Hofmeister's statements did not agree to this, but considered it to be of the eusporangiate type, the sporogenous tissue as arising from the division of a single cell but part of the walls and tapetum coming from the surrounding tissue. This is now the generally accepted view.

Goebel (1) gives an account of the development of the sporangium of *E. palustre* or *E. limosum* which he illustrates with two figures. According to this description it seems that the first division of the sporangial initial is periclinal and separates the primary sporogenous cell from the primary wall cell. In subsequent development the primary sporogenous cell divides much more rapidly than the other and we have a large mass of sporogenous tissue formed while a segment of the rather thin wall of the sporangium is all that comes from the primary wall cell.

This is one of the points where Bower (2) disagrees with Goebel. In his study of *E. arevense* and *E. limosum* he came to the conclusion that *Equisetum* is eusporangiate; that the contents of the sporangium are ultimately referable to a single initial; that the first division is periclinal, the inner cell and part of the outer going to form spores; and that the sporogenous tissue cannot be referred to a single cell as Goebel holds.

Campbell (3) does not seem to agree with Bower either as to the location of the superficial initial or as to its subsequent development. His account agrees more closely with that of Goebel. There appears no statement of the species he studied but it was probably *E. telmateia*.

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This is apparently all that has been published on the *sporangia* of the group up to the present time and it seemed that some of the other members should be studied in order to compare them with *E. limosum* and *E. arvense* as interpreted by Bower. *E. hyemale* L. was selected for examination and the sporangium studied, special attention being given to the younger stages.

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INVESTIGATION.

The material was gathered May, 1905 and 1906, near Sioux City, Iowa, along the north bank of a ravine in rather exposed places and on the north slope of a railroad grade. The killing solution used was a modification of Fleming's formula and was prepared as follows:

Chromic acid15 grams.
Acetic acid35 cubic centimeters
Water99. cubic centimeters

The siliceous protective leaves were removed before the young strobili were killed, they were run up through the alcohols in the usual manner and imbedded in paraffin with a melting point of 60 degrees C. The strobili were sectioned longitudinally, sections being cut seven mic. thick. The younger stages were stained in Delafield's haemotoxylin, the older in sanfranin gentian violet orange G. combination.

The young strobilus grows by means of an apical cell, cutting off alternate segments and these dividing both periclinally and anticlinally rather rapidly. No definite epidermal layer is differentiated. About the time the apical cell has advanced twelve or fourteen segments beyond a certain point and the outer cells have divided once or twice periclinally the papilla which is the young sporangiophore is noticeable. The first stages of this process are brought about by divisions in the hypodermal tissue and the outer layer does not seem to divide until there is a distinct protuberance. About this stage there is noticeable near the base of this papilla a cell (Fig. 10) with a large vesicular nucleus. It is somewhat larger than its fellows and its cytoplasm gives a peculiar reaction to the stain. It seems to agree rather closely with the initial figured by Bower for *E. arvense* and was thought to be homologous with it. It divides by a periclinal division forming an upper and a lower cell but in subsequent development only the upper cell functions in the formation of sporogenous tissue the lower one being sterile. In this paper therefore the upper and outer cell resulting from

this periclinal division is taken as the first cell of the sporangium, and its development will be traced as closely as possible.

The division of this first cell is anticlinal and may occur either radially to the sporangiophore (Fig. 3) or in a plane perpendicular to the radius (Fig. 2). But no case was found where it occurred periclinally. The second division takes place either periclinally or anticlinally and in either case the divisions in the two daughter cells are the same so that we have two plates of two cells each side by side. Further development of the sporangium takes place in various ways.

In general, however, the sporangia may be divided into two types which are correlated with the direction of this second division. It was noticed that when the wall was periclinal after a radial anticlinal division of the first cell, the sporangium formed was broad and rounded (Figs. 5, 14-18), while if the wall was anticlinal the sporangium was long and slender (Figs. 2-4, 6-13, 19).

The next division of the broad rounded type of sporangium, where the second wall is periclinal, is in the outer of the two pairs of cells which divide anticlinally (Fig. 5). These daughter cells may then divide either periclinally or anticlinally, the usual method, however, is for two or three walls to be formed anticlinally after which these cells divide (Figs. 14-16). The development of the inner cell is retarded (Figs. 15, 16) until about the time the tapetum is differentiated when it becomes active (Figs. 17, 18). The progeny of the outer cell does not divide as rapidly from now on as that of the inner cell. About this stage there is a differentiation of wall and tapetum and a little later the cells between the wall and tapetum become flattened along with the tapetum as the sporogenous tissue develops. The sporogenous tissue seems to come from both the inner and outer cells (Fig. 18).

The long slender type of sporangium, in which the second division is anticlinal, shows striking differences in development. The third division is periclinal and seems usually to be in the upper of the two pairs of cells (Fig. 6) both pairs, however, divide rather rapidly (Figs. 6-13) until in radial section there are two long rows of cells very separate and distinct from each other. When the number of cells in longitudinal section of the sporangium is about twelve or fourteen (Fig. 13) the tapetum begins to form and soon after, the cells of the sporogenous tissue begin to divide in the other direction also and a sporangium develops which compared with the other kind is rather long and slender (Fig. 19). This method of forming the sporangium does not seem to have been recorded by any who have worked on *Equisetum* though Bower mentioned that in *E. limosum* the development was somewhat irregular.

Later stages of the sporangium are similar to what Bower found for *E. limosum* and *E. arevense*. A large number of sporocytes are developed, about forty in radial section, many of which become disintegrated during the formation of tetrads.

The most striking difference is in the first stage of the sporangium. The large cell (Fig. 1) which cuts off the first cell of the sporangium is very sharply differentiated from its fellows by the size and structure of its nucleus and by the way its cytoplasm stains. The lower cell and its descendants are distinctly differentiated from the rest of the tissue through several stages of the sporangium. The outer half of the large cell, the first cell of the sporangium, always divides anticlinally which is contrary to the usual method of division of the sporangial initial in the Equisetales. Taking these facts into consideration together with the position of this large cell, the conclusion is reached that it is homologous with the sporangial initial figured by Bower for *E. arevense* and that in *E. hyemale* the sporogenous tissue comes entirely from the primary wall cell while the inner cell is sterile.

SUMMARY AND CONCLUSION.

1. *Equisetum hyemale* is of the eusporangiate type.
2. The sporogenous tissue comes from a single cell.
3. The first wall is periclinal the inner cell being sterile, while the sporogenous tissue comes entirely from the outer cell.
4. The tapetum comes from the cells surrounding the sporogenous mass.
5. There are two types of sporangia differing in development and governed by the direction of the second division.
6. Many of the sporocytes are disintegrated during the formation of tetrads.

BIBLIOGRAPHY.

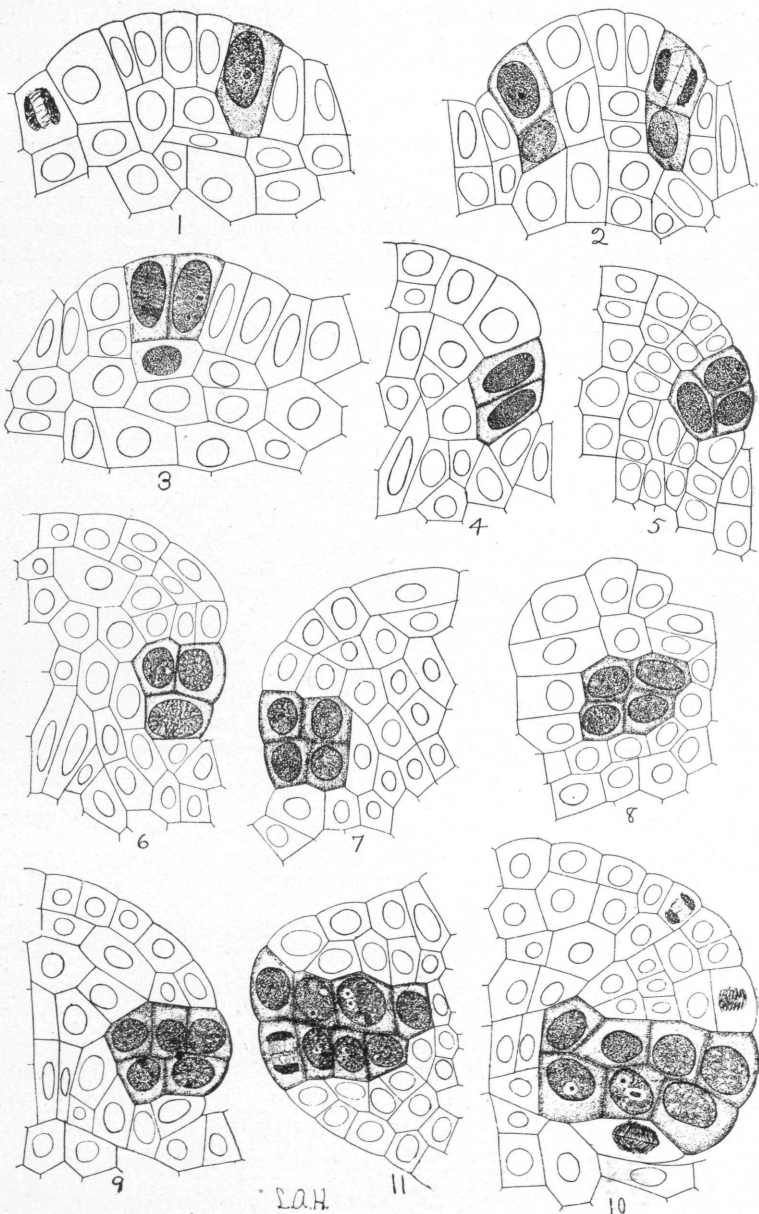
1. GOEBEL, K. "Beitrage zur vergleichenden Entwicklungsgeschichte der Sporangien." Bot. Zeit. 38:545.
2. BOWER, F. O. "Studies in the morphology of spore producing members. Equisetineæ and Lycopodineæ," Roy. Soc. Phil. Trans. 1894, page 473.
3. CAMPBELL, D. H. "Structure and Development of Mosses and Ferns," page 475.

EXPLANATION OF PLATES.

All figures were made with a Bausch and Lomb camera lucida and a Bausch and Lomb 1-12 oil immersion 1.32 N. a. objective with Leitz No. 4 ocular was used for all but Fig. 19 where a Leitz 1-7 objective with a No. 2 ocular was substituted. The original magnification was approximately 1500 diameters for all but Fig. 19 which was about 670 diameters. Drawings were reduced to one-fourth diameter of original magnification.

OHIO NATURALIST.

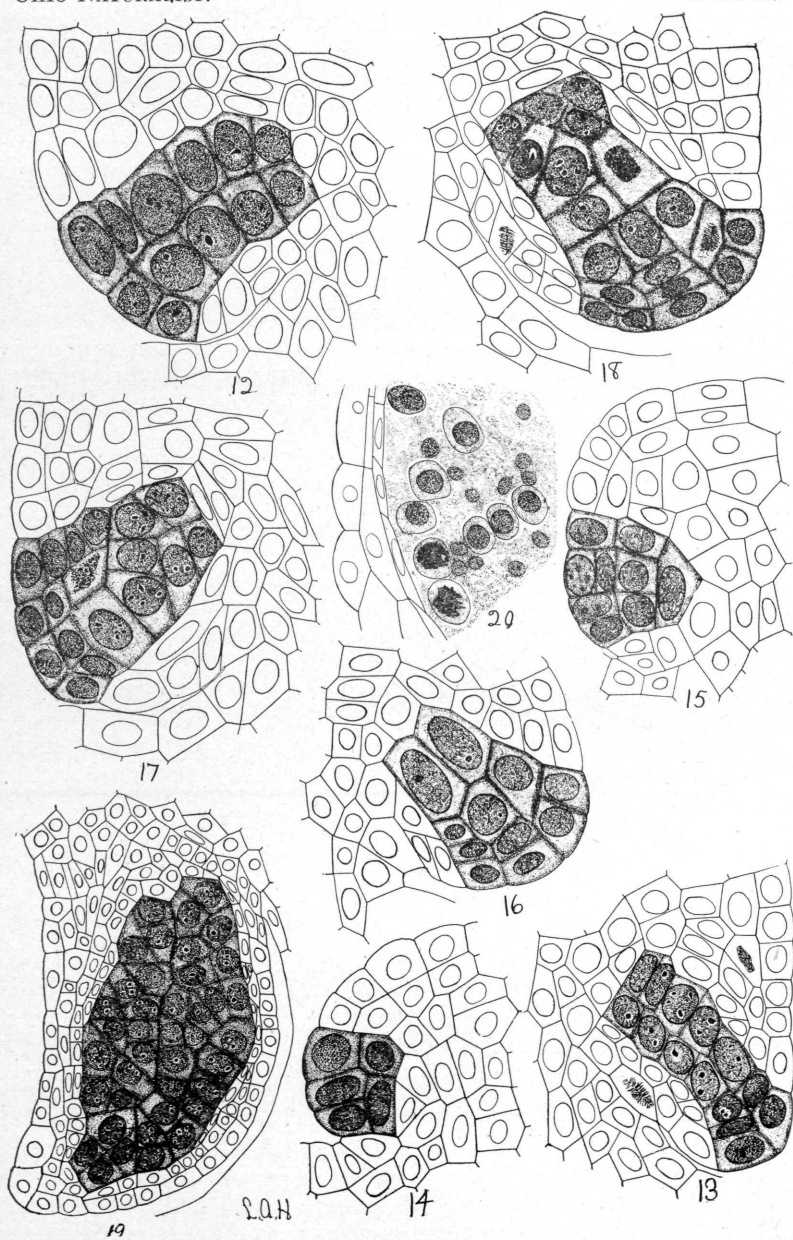
Plate IX.



HAWKINS ON "Equisetum."

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Plate X.



HAWKINS on "Equisetum."

Fig. 1. Incipient sporangiophore showing cell which will cut off the first cell of the sporangium.

Fig. 2. Young sporangiophore showing periclinal division and first anticlinal division perpendicular to a radius of the sporangiophore.

Fig. 3. Tangential view of a young sporangiophore in which the division of the first cell is radial.

Fig. 4. Radial view of four-celled stage of young sporangium, all divisions having been anticlinal.

Fig. 5. Radial view of six-celled stage of broad, rounded sporangium second division periclinal.

Figs. 6, 7. Radial views of six- and eight-celled stages of long, slender sporangia.

Fig. 8. Cross section of sporangium the same stage as Fig. 7 from an adjoining sporangiophore.

Figs. 9, 10. Radial sections of long, slender sporangia showing five and seven cells respectively.

Fig. 11. Longitudinal section of sporangium of the same type as Fig. 10 and from an adjacent sporangiophore, cut tangential to the strobilus.

Fig. 12. Later stage in the development of a long, slender sporangium; tapetum not yet differentiated.

Fig. 13. Section of long, slender sporangium, showing formation of tapetal layer; five outer cells slightly differentiated from the sporogenous tissue will form wall.

Fig. 14. Early stage in development of broad, rounded sporangium; the second division was probably periclinal.

Figs. 15, 16. Later stages in development of broad, rounded sporangia; the heavy lines indicate the position of the first periclinal division.

Fig. 17. Broad rounded sporangium, the tapetum beginning to form; the heavy line indicates the position of the first periclinal wall.

Fig. 18. Later stage in development of broad, rounded sporangium, the tapetum and wall differentiated and position of first periclinal division indicated by heavy line.

Fig. 19. Sporocyte stage of long, slender sporangium; the heavy line shows position of early anticlinal division.

Fig. 20. Section of older sporangium showing disintegrating sporocytes.